

MIDDLE EOCENE RODENTS (MAMMALIA)
FROM NORTHEASTERN UTAH

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INTRODUCTION

The first mention of fossil rodents from the Green River Formation in northeastern Utah was in Burke's preliminary report (1935) on two fossiliferous zones from which fossil mammals had been collected by field parties of Carnegie Museum. On the basis of these fossils the lower of the zones has been considered late Wasatchian in age and the upper, early Bridgerian. Rodents, "*Paramys* sp. (*hians* group)" and "*Sciuravus* (?) sp. nov." (Burke, 1935:13), occurred in the upper zone. The locality of the upper zone, known as "Powder Wash," is situated about two miles southeast of Powder Springs (sec. 8, T. 7 S., R. 25 E., S.L.M.), Uintah County, Utah, on the basin side of Raven Ridge in the eastern part of the Uinta Basin. The sandstone deposits containing the fossil mammals represent a deltaic facies of the Green River Formation (Kay, 1957:110). The locality is near the eastern margin of what was Lake Uinta, where fluctuations of that lake led to much interfingering of lacustrine and fluvial deposits at the lake's margin. Although much stratigraphic work has been done in the eastern Uinta Basin in relation to oil and gas fields, until recently no detailed stratigraphic studies had been made in connection with this precise locality. Now, however, W. B. Cashion, Jr., of the United States Geological Survey, has correlated the section containing the mammal quarry with more typical Green River deposits to the southeast. He reports that, "The Powder Wash mammal locality is about 270 feet stratigraphically below the Mahogany oil-shale bed and is in the Douglas Creek Member of the Green River Formation" (written communication, October 19, 1967). Thus the mammal quarry is near the lower part of the Green River Formation as it is developed in the eastern Uinta Basin.

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The fauna of the Bridgerian level, collected since 1931, is diverse, consisting of fishes, reptiles, and birds as well as marsupials, insectivores, primates, condylarths, a tillodont, rodents, carnivores, and perissodactyls. The fauna is, however, largely unstudied. Burke (1937) described a new sciuravid rodent from the locality, Gazin (1958) included the Powder Wash primates (calling the locality "Powder Springs") in his study of middle and upper Eocene primates, and Wood (1962:164, 241) mentioned a few rodent specimens from Powder Wash.

Over the years since the discovery of the mammal-bearing deposits at Powder Wash, J. LeRoy Kay, then Curator of Vertebrate Fossils, Carnegie Museum, collected material there and supervised its preparation, often ably assisted by A. C. Lloyd of this Museum. Thanks are due to them and to other members of Carnegie Museum field parties who maintained continued interest in the Powder Wash deposits. I have appreciated use of specimens in the care of C. Lewis Gazin, United States National Museum (USNM), Malcolm C. McKenna, American Museum of Natural History (AMNH), Elwin S. Simons, Yale Peabody Museum (YPM), and William D. Turnbull, Field Museum of Natural History (FMNH), and discussions of the rodents of Powder Wash with Craig C. Black, John Burke, and Albert E. Wood. Dr. Gazin helped to unravel some stratigraphic problems. Illustrations were skillfully prepared by Donald Rodkey. Measurements of *Paramys* and *Pseudotomus* were made with calipers, and those of the other rodents with an ocular micrometer disc. This study was supported by grants GB-1266 and GB-4089 from the National Science Foundation.

METHODS

COLLECTING AND PREPARING SPECIMENS

The bulk of the collections of Powder Wash vertebrates have come from quarries in a friable, yellowish sandstone, although anthills near the outcrops have yielded some fossils. Within the areas that have been quarried bones are often concentrated locally. Broken shafts of bird bones, lizard jaws, and mammal teeth are most common. Few mammals over the size of *Hyopsodus* are preserved, although *Orohippus* and *Hyrachyus* are represented by a few specimens, and the largest mammal present is a tillodont. Fragments of crocodylians, snakes, and turtles occur also.

The sandstone was removed from the quarries in medium-sized to

small pieces. The smaller pieces were sifted rather vigorously through window screen in a frame. Some specimens were recovered from the screen and pieces of sandstone showing promising concentrations of bone were taken to the Museum for further preparation. Part of the preparation was done manually, but much of the matrix was broken down by a freezing technique and then sorted for fossils. At present preparation is being done by means of a very dilute acid (e.g. citric) which makes the lightly cemented sandstone easily removable from the fossils.

Although the collecting and preparing techniques used have probably led to breaking of some specimens, unworked blocks from the quarries show that many of the unprepared fossils consist of broken pieces and isolated teeth. Very small lizard jaws are often preserved intact. Of the rodents a few relatively complete specimens are known, but the rodent record is based mostly on isolated teeth. It is likely that the bones were quite broken when deposited in this deltaic deposit, although most teeth are fresh in surface configuration and neither water worn nor abraded.

TAXONOMIC PROCEDURES

The rodents in the collections range in size from large (*Pseudotomus*) to tiny (*Pauromys*). One ischyromyid is known from a lower jaw and a maxillary fragment, as well as from isolated teeth. The rodent represented by the best material is *Sciuravus eucristadens*, a medium-sized form known from jaws and maxillae, mostly incomplete but nonetheless showing association of teeth. Of the smaller rodents only one is known from anything more than isolated teeth, the exception being the tiny rodent *Pauromys*, of which there is a maxillary fragment with M^{1-2} and an edentulous jaw as well as hundreds of isolated teeth.

Study of a record of this sort, based for some species on isolated teeth alone and including isolated teeth for all, is fraught with difficulties. Which molars were associated within one kind of jaw or maxilla? What was the dental formula? Which premolar or premolars, if any, pertain to which molars? Even, which upper teeth belong with which lowers? What sort of incisor belongs to each taxon?

Samples assigned to some species exhibit considerable individual variation. Is it accurate to assign the entire population to an already named species that some of the variants resemble? Is it misleading then to interpret that taxon on the basis of the material so prob-

lematically assigned? It is possible that rare species have been overlooked or considered simply variants of some of the more common species.

Because of these difficulties the taxonomic approach here used is a very conservative one. Several taxonomic assignments have been very tentatively given, a procedure here regarded as being preferable either to making definite assignments, perhaps incorrectly, to existing taxa, or to creating new taxa that cannot be distinguished adequately from existing ones. It is hoped that the rodents here described will prove sufficiently interesting in themselves to warrant these descriptions no matter what their specific assignments may be when the rodent record is more adequate.

SYSTEMATIC DESCRIPTIONS

Family ISCHYROMYIDAE¹ Alston, 1876

Paramys Leidy, 1871

Paramys near *P. delicatus* Leidy, 1871

Figures 1-4

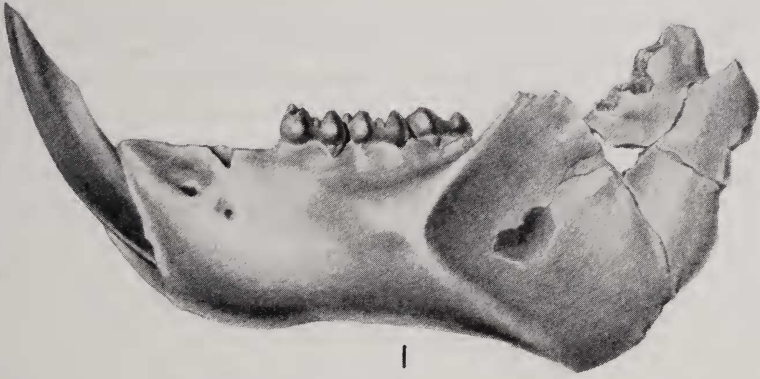
SPECIMENS: CM 11872, incomplete right maxilla, P⁴-M¹; CM 13000, left jaw, I, M₁₋₃; CM 13002, 13804, 13805, 13811, 13813, 13814, upper molars; CM 13803, 13809, 13812, upper premolars; CM 13001, 13033, 13810, lower molars; CM 13003-13005, 13806-13808, upper and lower deciduous teeth. Total isolated cheek teeth, 18.

DESCRIPTION AND DISCUSSION

Resemblance in jaw morphology, general shape of the lower incisor, and molar construction (figs. 1, 2) lead to comparison of this medium-sized rodent with *Paramys delicatus*. The Powder Wash specimens differ from *P. delicatus* as discussed by Wood (1962:29-33) in two main regards. First, the lower incisor is transversely narrower in the

¹ In the sense of Black, 1968; includes families Paramyidae and Ischyromyidae of Wood, 1955.

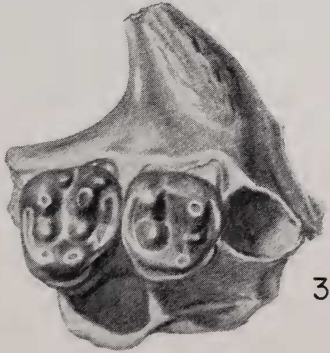
Fig. 1: lateral view of left jaw, approx. x2. Fig. 2: occlusal view of M₁₋₃, approx. x4. Fig. 3: CM 11872, occlusal view of right maxilla, P⁴-M¹, approx. x4. Fig. 4: CM 13004, occlusal view of right dP⁴, approx. x8. Figs. 5, 6: occlusal views of teeth of *Pseudotomus* near *P. robustus*, approx. x6. Fig. 5: CM 13802, right upper molar. Fig. 6: CM 13800, left M³.



1



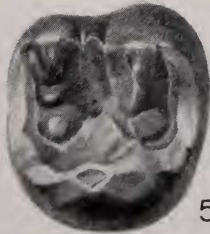
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5



6

Powder Wash form. As in *P. delicatus* the ventral (or anterior) side is slightly grooved, and the general shape is not too different from that of some variants among *P. delicatus*. In its narrowness the incisor approaches that of some early Eocene species, such as *Paramys major*. Second, the Powder Wash specimens tend toward smaller size than in Wood's sample of *P. delicatus* (1962, tables 2, 3). The size of the lower teeth is near the lower observed range of Wood's sample and is smaller than his mean in every case. Upper teeth (figs. 3, 4) from Powder Wash, both deciduous and permanent, differ even more from Wood's sample, being slightly below his observed ranges for most teeth. The Bridgerian *Paramys delicatior* is also smaller than *P.*

TABLE 1
MEASUREMENTS (IN MM.) OF *Paramys* NEAR *P. delicatus*

	CM 11872	CM 13004	CM 13000	CM 13808
P ⁴ anteroposterior	3.5			
width	4.1			
M ² anteroposterior	3.6			
width	4.4			
dP ⁴ anteroposterior		3.3		
width		3.6		
M ₁ anteroposterior			4.0	
width trigonid			3.6	
width talonid			3.9	
M ₂ anteroposterior			4.2	
width trigonid			3.8	
width talonid			4.2	
M ₃ anteroposterior			4.9	
width trigonid			-	
width talonid			3.8	
dP ₄ anteroposterior				3.4
width trigonid				2.1
width talonid				2.7

delicatus but has an even wider lower incisor than in *P. delicatus*, lacks the groove in the incisor, and has a coronoid process more anteriorly situated than in the Powder Wash jaw.

At present the taxonomic reference for this rodent is left indefinite, so as neither to mask the differences of the Powder Wash *Paramys* from Bridger Basin specimens nor to establish a distinct taxon for what may prove to be only an inseparable segment of the *P. delicatus* population.

Pseudotomus Cope, 1872

Pseudotomus near *P. robustus* (Marsh, 1872)

Figures 5, 6

SPECIMENS: CM 13800, 13802, 19560, upper molars; CM 13801, 13007, lower molars.

DESCRIPTION AND DISCUSSION

The five molars representing a large manitshine are generally similar in morphology to those of Bridgerian specimens of *Pseudotomus* and *Ischyrotomus* (Wood, 1962: 182-186, 201-211). It can be seen that, in a relatively early stage of wear (figs. 5, 6), upper molars have multiple conules. The enamel is slightly rugose within the basins. The size of these teeth is less than in *Pseudotomus robustus*, *Ischyrotomus horribilis*, and *I. oweni*, the Bridgerian manitshines known from molar teeth. In presence of multiple conules on the lophes of the upper molars, as well as in size, the Powder Wash manitshine approaches a Wasatchian species, *Pseudotomus coloradensis*.

The type species of *Pseudotomus*, *P. hians*, is based on a skull having the incisors but lacking cheek teeth. *Pseudotomus robustus* has a type consisting of two isolated cheek teeth and is known also from referred jaws, maxillae, and skeletal parts. The Bridgerian species *Ischyrotomus horribilis* is very similar to *Pseudotomus* and has been separated from that genus rather arbitrarily (Wood, 1962:201). The Bridgerian *I. oweni* is quite similar in dental characters to *I. horribilis*, although it seems to show a few features intermediate between *I. horribilis* and the Uintan *I. petersoni*, type species of the genus. Teeth of most previously known specimens of these two genera are usually worn, so that little remains of the pattern, which might have aided in differentiating species. In view of the great difficulty of distinguishing Bridgerian *Pseudotomus* and *Ischyrotomus* from one another, if indeed they should be generically separate, and of the inadequacy of

the Powder Wash manitshine specimens, a definite taxonomic reference cannot be provided. Reference is made to *Pseudotomus* near *P. robustus* rather than to *Ischyrotomus* near *I. horribilis* largely because *Pseudotomus* is the older name for Bridgerian manitshines and might prove in the long run to be the only valid one for that time interval. This reference to *Pseudotomus* is supported also by the presence of multiple conules in the upper teeth and smaller size than in either *P. robustus* or *I. horribilis*, characters in which the Powder Wash manitshine approaches *P. coloradensis*.

TABLE 2
MEASUREMENTS (IN MM.) OF *Pseudotomus* NEAR *P. robustus*

	Anteroposterior	Width	
CM 13802 upper molar	4.6		5.2
CM 13800 M ³	4.5		4.7
CM 13801 lower molar	4.7	4.2(trigonid)	4.8(talonid)
CM 13007 M ₃	5.5	4.8(trigonid)	4.4(talonid)

Microparamys Wood, 1959

The genus *Microparamys* ranges throughout the Eocene in North America and is known from the early and middle Eocene of Europe. Understanding of the small rodents referred to the genus is hampered by the very sparse material on which most of the species are based. It is recognized, however, that the genus as now constituted is a composite of small rodents that may or may not be closely related (Wood, 1962:158; Thaler, 1966:18). Of the species now known and referred here, it appears likely that the North American species, *M. minutus*, *M. tricus*, *M. dubius*, and *Microparamys* sp. A and D (Wood, 1962:160, 165), form an associated unit. It is also likely that the European species, *M. nanus*, *M. russelli* (Michaux, 1964:154), and *M. monspeliensis* (Thaler, 1966:18-20) belong here. Other species assigned to *Microparamys* are of more doubtful affinities. *Microparamys wilsoni* might be referable to the preceding group, but the worn teeth of the type specimen offer few morphological details on which close determination of affinities can be made. The maxilla with P⁴, YPM 13451, referred to *M. wilsoni* (Wood, 1962:164-165), differs from other *Microparamys* in the structure of P⁴ and the probable enlargement of M¹, but materials are inadequate to determine whether the association of jaw and maxilla is correct. If the maxilla is properly

referred, it is probable that *M. wilsoni* is not closely allied to the preceding group, and is not referable to *Microparamys* at all. Other species, including Wood's "forms of larger size, with less development of the microparamyine tooth specialties" (1962:158), are of still more dubious reference to the genus. Of them, *M. lysitensis* and *M. cathedralis* of the early Eocene are poorly known, the former from a few jaws and lower teeth, some fragments of upper teeth, and some incisors (Wood, 1965:124-125), and the latter from one jaw with rather worn teeth. It is likely that the three upper teeth referred to the middle Eocene *M. wyomingensis* (Wood, 1959b:163) do not represent *Microparamys*. The two P⁴ considered by Wood (1962:164) to be *Microparamys* sp. C belong to *Sciuravus eucristadens* (see below).

As the record stands the most adequately known species of *Microparamys* is *M. tricrus* of the late Eocene of southern California, represented by a maxilla having P⁴-M² and a jaw having P₄-M₃. Although the fossil record for small rodents, such as the various species of *Microparamys*, may never be very good, the current collecting techniques of washing and screening should improve the representation of teeth of rodents of this size, if not the completeness of individual specimens. The sample of *Microparamys* from Powder Wash is composed of about 120 isolated teeth including P⁴-M³, P₄-M₃, and some probably referable incisors and deciduous teeth. The species seems to be *M. minutus*, which is otherwise known from a few partial lower jaws, some isolated lower teeth, and one upper molar from the Bridger Basin.

Microparamys minutus (Wilson, 1937)

Figures 7-18

SPECIMENS: CM 13014, P⁴; CM 13009, 13010, 13012, 13013, 13015, 13019, 13832, M¹⁻²; CM 13011, 13021, 13037, 13833, M²; CM 13036, 13830, 19636, P₄; CM 13022-13024, 13028, 13031, 13834, M₁₋₂; CM 13025, 13027, 13827, 13829, M₃. Possibly referable, CM 13831, 19638, dP⁴; CM 13018, 19637, dP₄.

DESCRIPTION

This species is close in size to the unnamed sciuravid in the Powder Wash fauna. In the case of molars there are enough characters to differentiate the two taxa, but permanent and especially deciduous premolars and incisors are more of a problem. Molars of *Microparamys* are smaller than those of the sciuravid and the premolars here referred are likewise smaller.

UPPER CHEEK TEETH: No P^3 is known. The somewhat triangular P^4 (figs. 7, 8) has weak lophs from paracone and metacone to the protocone. A metaconule swelling occurs on the loph from the metacone. Usually some trace of a mesostyle is present between paracone and metacone. The anterior cingulum is short transversely. A hypocone is present but weak.

The first two molars, which are difficult to differentiate from one another, have an essentially quadrate shape (fig. 9). The basic impression given by the pattern is of a triangle formed by lophs from paracone and metacone converging on the protocone. These lophs are subdued in most specimens and appear to have been worn down rapidly. In little-worn M^{1-2} one or two metaconules occur on the loph from the metacone, but these become indistinct following wear. The hypocone is a discrete cusp. In some little worn specimens a crest extends from the hypocone toward the loph from the metacone but lacks a contact with this loph. A small mesostyle is present. The distinct anterior cingulum is separated buccally and lingually from paracone and protocone. The posterior cingulum extends to the hypocone.

An upper molar, YPM 13452, was referred by Wilson (1937:454) and Wood (1962:160, fig. 54E) to *M. minutus*. This M^1 or M^2 is larger relative to the lower teeth of the type specimen of *M. minutus* than upper molars of Powder Wash *Microparamys* are to the corresponding lower molars (see table 3). In addition, YPM 13452 differs from the Powder Wash sample of M^{1-2} in having accessory ridges in the central basin and a stronger crest from the hypocone. The stratigraphic levels within the Bridger that produced the type lower jaw and the referred upper molar are unknown, and perhaps the size difference indicates some change through time.

Because M^3 is absent in previously reported *Microparamys* there is some uncertainty as to which of the M^3 in the Powder Wash sample should be referred here. The teeth that seem most probably referable are variable but usually more or less elongated posteriorly (figs. 10, 11). These teeth have a well developed anterior cingulum, distinctly

Figs. 7-18: Occlusal views of teeth of *Microparamys minutus*. Fig. 7: CM 19565, right P^4 . Fig. 8: CM 13017, right P^4 . Fig. 9: CM 19564, left upper molar. Fig. 10: CM 19562, left M^3 . Fig. 11: CM 19563, left M^3 . Fig. 12: CM 19636, right P_4 . Fig. 13: CM 13029, right lower molar. Fig. 14: CM 13031, left lower molar. Fig. 15: CM 19566, right lower molar. Fig. 16: CM 19567, left M_3 . Fig. 17: CM 19638, right dP^4 , probably *M. minutus*. Fig. 18: CM 19637, right dP_4 , probably *M. minutus*. Figs 7, 9-11, 13-16, approx. x15; figs. 8, 12, 17, approx. x20; fig. 18, approx. x25.



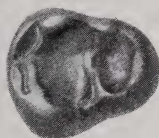
7



8



9



10



11



12



13



14



15



16



17



18

cuspsate protocone and paracone connected by a loph, and a mesostyle. The metacone is not distinct from the posterior cingulum, and the various other cusps are incorporated in the cingulum also. The talon of M^3 varies not only in degree of posterior elongation but also in development of accessory cusps and ridges within the basin. A posteriorly elongated M^3 occurs in several other Eocene rodents, being prominent in the early Wasatchian species *Franimys amherstensis* and in an early Wasatchian specimen of *Paramys excavatus* (Wood, 1962:54, fig. 48E). Variable elongation of M^3 occurs in the late Wasatchian *Thisbemys nini* (Wood, 1962:110), and the tooth also is somewhat elongate in the Bridgerian *Reithroparamys delicatissimus*.

LOWER CHEEK TEETH: The lower premolars (fig. 12) that seem referable to *Microparamys* are similar in general to the premolar of *M. minutus* shown by YPM 13450. The posterior protoconid arm closes the trigonid valley posteriorly. A distinct mesoconid occurs on the ectolophid. The small entoconid either lacks a crest or has one slightly developed and extending toward the posterior cingulum.

The Powder Wash specimens of M_{1-2} (figs. 13, 14), though basically like those teeth of previously known *M. minutus*, exhibit variations that are unknown among the smaller sample of individuals from the Bridger Basin. The entoconid crest varies from well developed to essentially absent. In most specimens the posterior protoconid arm is longer than in the type of *M. minutus*, YPM 10730. In nine out of 39 M_{1-2} the metastylid occurs as a discrete stylid, whereas in the remaining 30 teeth there is either an elongated ridge forming the posterolingual slope of the metaconid or no trace of metastylid and ridge. Both stage of wear and individual variation are probably involved in these dental variants. One lower molar (fig. 15) has two cusps in the normal position of the entoconid (a "twinned" entoconid perhaps), one cusp is lingual and slightly anterior to the lingual end of the posterior cingulum, and the second is more anterolingual in position.

On M_3 (fig. 16) the metaconid is a very prominent cusp. As in M_{1-2} , in early wear the buccal end of the anterior cingulum is separate from the protoconid. The posterior arm of the protoconid varies from long to short. A mesoconid is present. Out of 12 specimens of M_3 having the region preserved, seven have a cuspsate metastylid. In the others the metaconid is ridged posterolingually. The entoconid is a distinct cusp but is met posteriorly by the posterior cingulum. Usually the entoconid lacks a crest, although a few specimens show a

faint suggestion of entoconid cresting. In *M. tricus* the entoconid is crested and the talonid of M_3 is more elongated posteriorly than in *M. minutus*. In some specimens from Powder Wash a slight swelling on the posterior cingulum suggests presence of a hypoconulid.

Several transversely narrow lower incisors resembling those in the type of *M. minutus*, YPM 10730, appear referable here, and some deep, narrow, upper incisors are probably also referable. However, it is very difficult to separate broken incisors of *Microparamys* from some, slightly thicker transversely, that may represent the unnamed small sciuravid in the fauna.

Out of ten probable dP^4 , eight have a pattern showing lophs from paracone and metacone that converge on the protocone (fig. 17). There is a definite hypocone on these teeth, which may represent *Microparamys*. The two remaining dP^4 are slightly larger and have the loph from the metacone crossing the tooth more transversely toward the area of the hypocone. The hypocone is not a distinct cusp in these two, which might represent the unnamed sciuravid (fig. 38). Neither reference is definite enough to allow much weight to be placed on evidence from these teeth.

Similar difficulty of differentiating between *Microparamys* and the sciuravid apply to the nine specimens of dP_4 . The two largest specimens are more elongate than the others and seem to have a more medially situated ectolophid, as in the sciuravid. There is a great deal of pattern variation among the other specimens, and although some of the smaller dP_4 may represent *Microparamys* (fig. 18), no definite reference is made here for them.

DISCUSSION

The sample of *Microparamys* from Powder Wash includes specimens that are very close to previously known *M. minutus* from the Bridger Basin, as well as dental variants not known from the smaller Bridger sample. Resemblance seems to be close enough to allow reference to the Bridger Basin species. The Powder Wash specimens contribute new evidence on several features that are distinctive for the genus.

Wood (1962:158) considered the *Microparamys* group to be well separated from his *Paramys excavatus* species group. The separation seems to be lessened by similarity in M^3 between some members of the *P. excavatus* group and *Microparamys*. The primitive rodent *Franimys* is also close to *Microparamys* in this feature, as are some

Wasatchian specimens of *Thisbemys*. The elongation of M³ may be merely a character primitive for rodents.

The *Microparamys* line probably originated early in the Eocene from a group that may have led to varied lines of later rodent evolution, including that of the sciuravids.

TABLE 3
MEASUREMENTS (IN MM.) OF *Microparamys minutus*

Upper teeth	YPM 13452	YPM 13450	CM 19636	CM 13024	CM 13028	CM 13029	CM 13031	CM 19566	CM 19567
P ⁴ anteroposterior						.99	1.12		
width						1.24	1.36		
M ¹ or M ² anteroposterior	1.40	1.18	1.15	1.18					
width	1.71	1.24	1.21	1.40					
M ³ anteroposterior								1.30	1.36
width								1.08	1.21
Lower teeth	YPM 10730	YPM 13450	CM 19636	CM 13024	CM 13028	CM 13029	CM 13031	CM 19566	CM 19567
P ₄ anteroposterior		1.21	1.18						
width trigonid		.99	.81						
width talonid		1.09	1.05						
M ₁ anteroposterior	1.30	1.21							
width trigonid	1.01	1.15							
width talonid	1.30	1.24							
M ₂ anteroposterior	1.40								
width trigonid	1.27								
width talonid	1.40								
M ₃ anteroposterior									1.43
width trigonid									1.30
width talonid									1.27
M ₁ or M ₂ anteroposterior				1.24	1.24	1.30	1.36	1.33	
width trigonid				1.05	1.18	1.27	1.30	1.33	
width talonid				1.21	1.30	1.40	1.43	1.52	

TABLE 3, Cont'd.

Deciduous teeth	CM 19638	CM 19637
dP ⁴ anteroposterior	1.05	
width	1.08	
dP ₄ anteroposterior		1.18
width trigonid		.68
width talonid		.93

Family SCIURAVIDAE Miller and Gidley, 1918

Perhaps the most significant evidence to come from the Powder Wash rodents is that yielded by the Sciuravidae, especially the unnamed sciuravid and *Pauromys*. These two taxa exhibit a pattern of the upper molar teeth that was previously unknown in Bridgerian rodents and only suggested by the early Eocene genus *Knightomys*. Of these Powder Wash taxa, *Pauromys* is closer to *Knightomys* in the pattern of the lower teeth, whereas the unnamed sciuravid more closely resembles *Sciuravus* in this regard. The third sciuravid, *Sciuravus eucristadens*, has the upper molar pattern typical of other species of *Sciuravus* but has premolar specializations suggesting affinity with the Uintan *S. powayensis*.

Sciuravus Marsh, 1871

This Eocene genus is known from species ranging in age from late Wasatchian to Uintan. Two species occur in the Bridgerian of the Bridger Basin, *S. nitidus* and *S. bridgeri*. The former ranges through the Bridgerian and as now defined encompasses specimens showing a wide range of variation. *Sciuravus bridgeri*, which is known only from the early Bridgerian, is a smaller rodent and less abundantly represented in museum collections. A third species, ?*Sciuravus rarus*, was tentatively referred to the genus (Wilson, 1938:136-137).

A further species, *S. eucristadens*, was described on the basis of a lower jaw having M₁₋₃, from the sandstone deposits in Powder Wash (Burke, 1937). The incomplete material on which the species was based did not lead to a very clear understanding of the relationships of this species, although Wilson (1940:90, 1949:98) pointed out some interesting points of resemblance to the Uintan *S. powayensis* from

California. Fortunately *S. eucristadens* is now better known, being the rodent from Powder Wash that is best represented in terms of complete jaws and maxillae. These topotype specimens, collected since Burke established the species, add to the known morphology of this rodent and to the understanding of its relationships.

Sciuravus eucristadens Burke, 1937

Figures 19-25

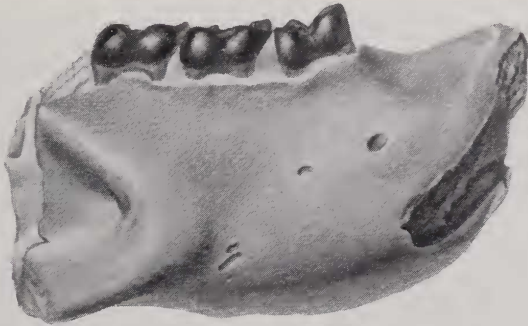
TYPE SPECIMEN: CM 11871, right jaw with I, M₁₋₃.

REFERRED SPECIMENS: CM 6481, maxilla and jaw associated; CM 5435, 6430, 6471, 6478, 6479, 13044, 13046, 13771, 19579, maxillae with teeth; CM 6429, 6472, 6475, 6498, 9469, 13058, 13060, 13061, 13066, 13077, 13079, 13793, jaws with teeth; CM 6483, 6484, 6487, 6489, 13032, 13041, 13042, 13045, 13047, 13049-13053, 13055-13057, 13207, 13762-13765, 13767, 13769, 13770, 13772, 13773, 13795-13797, 13799, 19580, FMNH 1205, 1206 (*Microparamys* sp. C of Wood, 1962:164), 1207-1209, 1211, isolated upper teeth; CM 13059, 13062-13065, 13067, 13068, 13070-13076, 13078, 13080-13083, 13085-13089, 13091, 13196, 13200, 13202-13204, 13777-13788, 13790-13792, 13798, 19561, FMNH 1196-1202, isolated lower teeth; CM 6482, 13043, 13206, 13766, 13768, 13794, 13822, dP⁴; CM 13201-13205, 13790, 13798, dP₄; CM 19577, upper incisors; CM 19578, lower incisors. Total isolated cheek teeth, about 235.

The main characters used by Burke (1937) to differentiate this species from *S. nitidus* were: central valley crowded, relatively wide posterior valleys in M₁ and M₃; stylids absent from exits of external and central valleys; cusps and crests robust, predominant over basins. Burke also discussed distinctive characters of M₃ in CM 11871, although he recognized that this tooth is highly variable in *Sciuravus* and that a more complete series might alter his interpretation of the characteristics of M₃ in *S. eucristadens*.

DESCRIPTION OF NEW MATERIAL

LOWER JAW AND DENTITION: The jaw of the type specimen, CM 11871, which represents a young individual, is dorsoventrally shallower than in older individuals represented by CM 13060 and 13061 (fig. 19) but resembles that in CM 13079, another young individual having P₄ unerupted. The young individuals have a transversely narrower incisor than do older ones. An adult lower incisor (fig. 20) is flattened ventrally (anteriorly), tapers dorsally, and has a slightly convex lateral side. On the jaw a mental foramen occurs in a line below or slightly anterior to P₄ and a second, smaller foramen is usually present behind the first. The masseteric fossa extends forward to a line below the



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Fig. 19: *Sciuravus eucristadens*, CM 13061, lateral view of right jaw, approx. x5.

trigonid of M_2 or talonid of M_1 , and the ridge ventral to the fossa is stronger in older specimens than in CM 11871.

The lower premolar (fig. 21), absent in the type specimen, has a trigonid with a prominent metaconid and less elevated protoconid. In early wear the trigonid valley has an anterobuccal exit. Several relatively unworn specimens have a small cingulum anterior to the metaconid on P_4 . Protoconid and hypoconid are crowded but between them is a short ectolophid on which there is a rounded mesoconid. In most specimens of P_4 that show relatively unworn lophs, the hypolophid extends from hypoconid to entoconid and the posterior cingulum is separate from this at the posterior edge of the tooth. A few specimens show the entoconid crest bending back to contact the cingulum. P_4 is smaller relative to M_{1-3} than in *S. nitidus*, but *S. eucristadens* resembles *S. powayensis* in size of P_4 relative to the molars and in the usually transverse hypolophid. The jaw of *S. powayensis* shows some advance beyond that of *S. eucristadens* in having a slightly more anterior position of the masseteric fossa.

Little can be added to Burke's (1937:2-4) detailed description of M_{1-2} except mention of variations. Stylids are occasionally present. They are found outside the ectolophid and a metastylid occurs on M_{1-2} as well as on P_4 . Generally, however, these are absent as on the type specimen. The mesoconid is usually rounded or only slightly elongated transversely and does not have the medially extending ridge that is often found in *S. nitidus*. The appearance of the molars, described by Burke (1937:2) as having the "cusps and crests in general robust, predominant over basins" is somewhat reminiscent of

the molars of the late Wasatchian species, *S. wilsoni* (Gazin, 1962, pl. 4, fig. 6).

On M_3 the mesoconid is usually more elongated lingually than on M_{1-2} . The pattern of M_3 described by Burke appears as does a variant with little or no development of the cuspule and accessory ridges on the hypolophid. In other specimens of M_3 the entoconid crest extends toward or to the hypoconid rather than to the mesoconid-ectolophid.

The lower deciduous premolar (fig. 22) is relatively longer and narrower than P_4 , having an elongated central valley. Ectolophid and mesoconid are weakly developed. Posterolingually the metaconid is extended by a ridge on which a metastylid is present in some specimens. The hypolophid is strong and, as on the molars, is straight from hypoconid to entoconid. A short anterior cingulum, or anteroconid, is present anterior to the anterior exit of the trigonid valley.

MAXILLA AND UPPER DENTITION: The anterior zygomatic root extends out with its posterior edge on a line with P^3 . The zygoma is ridged ventrally, the ridge terminating anteroexternal to P^3 in a slightly rounded knob. Basically the zygoma and intraorbital foramen resemble those in *S. nitidus*. In *S. powayensis* the ventral ridge and knob are more prominent.

Only one specimen of P^3 , CM 19580, has been found. As in P^3 of *S. nitidus* the tooth has an anterobuccal peak, central depression, and posterolingual low cingulum.

The most distinctive upper tooth is P^4 (fig. 24). On this tooth paracone and metacone are crowded together, and there is no mesostyle. An anterior cingulum is present, and the metaconule is distinct. In some specimens the paracone is situated approximately in the middle of the tooth's buccal side, with the metacone close behind it. The metacone-metaconule loph is directed essentially transversely. Some indication of a hypocone is present, usually only a swelling on the posterior cingulum. In *S. powayensis* the buccal cusps on P^4 are crowded somewhat similarly to those in *S. eucristadens* and the metacone-metaconule forms a short, transversely directed loph. The



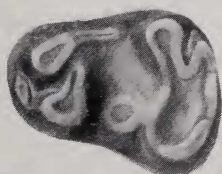
Figs. 20-25: Teeth of *Sciuravus eucristadens*. Fig. 20: CM 6498, cross-section of left lower incisor. Figs. 21-25, occlusal views of teeth. Fig. 21: CM 6498, left P_4 - M_1 . Fig. 22: CM 13204, left dP_4 . Fig. 23: CM 19639, left M^3 . Fig. 24: CM 6471, right P^4 - M^2 . Fig. 25: CM 13206, right dP^4 . Figs. 20, 21, 23, 24, approx. x10; figs. 22, 25, approx. x15.



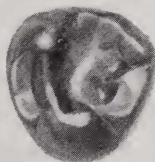
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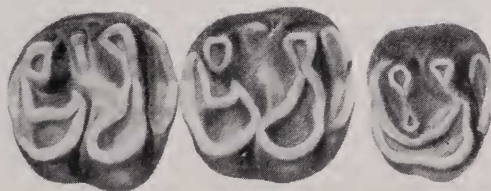
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two teeth referred by Wood (1962:164) to *Microparamys* sp. C are characteristic specimens of P⁴ of *S. eucristadens*.

The upper molars are quite similar to those in *S. nitidus*. On M¹⁻² anterior and posterior cingula are well developed, a mesostyle is present, and protocone and hypocone are subequal. On M¹ the loph from the protocone usually ends slightly anterior to the paracone, whereas on M² it extends to the paracone. A loph from the hypocone extends anterobuccally, then bends posterobuccally toward the metacone. The posterobuccally directed limb of this loph is usually weakly developed. In one specimen, CM 13056, a small cusplule occurs on the medial flank of the metacone. On M³ (fig. 23) the mesostyle is less well developed than on M¹⁻² and the talon is relatively smaller, although a hypocone and a metacone, which is connected by a crest to the metaconule, can be differentiated in early wear.

The fourth upper deciduous premolar (fig. 25) is slightly smaller and more molariform than P⁴, having a better developed anterior cingulum, a distinct hypocone well separated from the protocone, and complete proto- and metalophs. The protoconule is smaller than the metaconule but both are distinct in unworn dP⁴.

The upper incisor is slightly narrower than the lower incisor. The fairly straight sides are inclined toward one another posteriorly.

DISCUSSION

This topotype material of *Sciuravus eucristadens* allows the following emended diagnosis to be made for the species:

Species of *Sciuravus* having P¹ with more closely spaced paracone and metacone than in *S. nitidus*, and metacone-metaconule loph transversely directed; lower molar cusps and crests robust, predominant over basins; P₄ with well developed entoconid crest, usually contacting hypoconid; masseteric fossa extends to line below trigonid of M₂ or talonid of M₁; size near *S. nitidus*, larger than *S. powayensis*.

Characters of the premolars of *S. eucristadens* add to the points of resemblance given by Wilson (1940:90) between *S. powayensis* and *S. eucristadens*. The premolars are small relative to the molars, although this size reduction has gone farther in *S. powayensis*. As in *S. powayensis* the paracone and metacone of P⁴ are close to one another and the metaloph is transversely directed. The entoconid of P₄ is usually crested in *S. powayensis* and in some specimens connects with the hypoconid, further resemblance to *S. eucristadens*.

The Powder Wash specimens of *S. eucristadens* can be used to demonstrate some problems that arise when only isolated teeth are

TABLE 4
MEASUREMENTS (IN MM.) OF *Sciuravus eucristadens*

	CM 6430	CM 6471	CM 19639	CM 13206	CM 11871	CM 6498	CM 13061	CM 13079	CM 13204
P ⁴ anteroposterior		1.70							
width		2.02							
M ¹ anteroposterior	2.14	2.14							
width	2.39	2.27							
M ² anteroposterior	2.14	2.14							
width	2.46	2.39							
M ³ anteroposterior	2.08		2.02						
width	2.33		2.10						
dP ⁴ anteroposterior				1.72					
width				1.60					
P ₄ anteroposterior						1.95	1.89	-	
width trigonid						1.39	1.39	1.39	
width talonid						1.51	1.64	1.39	
M ₁ anteroposterior					2.20	2.20	2.14	2.27	
width trigonid					1.45	1.58	1.76	1.64	
width talonid					1.70	1.95	1.95	1.83	
M ₂ anteroposterior					2.08		2.27	2.33	
width trigonid					2.02		2.02	2.08	
width talonid					2.02		2.14	2.27	
M ₃ anteroposterior					2.84			2.65	
width trigonid					2.14			2.14	
width talonid					2.27			2.02	
dP ₄ anteroposterior									1.93
width trigonid									1.17
width talonid									1.50
Lower incisor width					1.07	1.51			
Depth jaw at M ₁					5.24		6.40		

known. On the one hand, Wood made too great a taxonomic separation by regarding isolated premolars of *S. eucristadens* as referable to *Microparamys*. On the other, had *S. eucristadens* been known from isolated teeth alone, the distinctive characters of the premolars might have been overlooked and the teeth not differentiated from those of *S. nitidus*. These two errors, one of making too great a split based on isolated teeth and the other of making too little differentiation for a taxon, occur easily if only isolated teeth are known. Fortunately, this interesting sciuravid is now more adequately known and can be distinguished as a distinct taxon that shows some approach to the Uintan species, *S. powayensis*.

Sciuravid sp.

Figures 26-38

SPECIMENS: CM 13039, 19615, P⁴; CM 13208-13213, 13218; FMNH 1210, M¹⁻²; CM 13821, 19616, M³; CM 19583, 19643, dP⁴; CM 13823, 19617, P₁; CM 13026, 13195, 13214-13217, 13824, M₁₋₃; CM 13825, 19614, 19645, M₃; CM 19584, dP₄; CM 19581, 19582, incisors.

This sciuravid, which is smaller than *Sciuravus eucristadens* but slightly larger than *Microparamys minutus*, has lower molars that are generally similar to those of *S. bridgeri*, a species known from lower jaws and teeth from the early Bridgerian of the Bridger Basin (Wilson, 1938:133-136). The Powder Wash sciuravid is known only from isolated teeth but both upper and lower teeth are represented.

DESCRIPTION

LOWER CHEEK TEETH: As mentioned in the description of *Microparamys*, the premolars of *Microparamys* and this sciuravid might be confused with one another. The following description of P₄ (figs. 26-28) is based on the larger premolars that seem referable here. In the worn condition the trigonid of P₄ is dominated by the metaconid. The protoconid is little more than a worn area on the buccal flank of the metaconid. In earlier wear the protoconid is a small cusp, connected posteromedially to another cuspule that blocks but does not close the trigonid valley posteriorly. An anteroconid occurs anteriorly in the valley. The ectolophid is more medially situated than on P₄ assigned to *Microparamys*. The talonid, wider than the anteriorly tapered trigonid, has a small but distinct and crested entoconid. A hypoconulid swelling occurs on the posterior cingulum. The premolars are smaller relative to M₁ than is P₄ in the type specimen of

Sciuravus bridgeri, USNM 12141, and the protoconid is much less well developed. Two specimens of P_4 in early-wear stages that might be referable to this sciuravid resemble the more worn teeth in having a well elevated metaconid and other features, but are distinct in having an anterior cingulum anterobuccal to the protoconid.

The first two molars (figs. 29, 30) are similar to one another in cusp pattern but differ somewhat in shape, the trigonid of M_1 being narrower relative to the talonid, whereas M_2 is more quadrate in outline. On both teeth the metaconid is the most prominent and projecting cusp. Its posterior side descends steeply into the central valley. In most cases the metaconid is ridged posterolingually, and in some specimens one or two stylids occur on the ridge. Unworn and little worn M_{1-2} have a small cingular cusp blocking the anterior exit of the trigonid valley. Lingually this cusp extends into a crested cingulum. The posterior arm of the protoconid reaches toward the posterior flank of the metaconid and is variable in length, ranging from relatively short to crossing more than half the width of the tooth. A small mesoconid is present on the ectolophid, and in at least one specimen a short ridge extends lingually from the mesoconid. The hypoconid is connected posterolingually with the posterior cingulum, which in less worn specimens shows a distinct hypoconulid. The entoconid, a small cusp relative to the metaconid, has a buccal crest that extends to or toward the hypoconid or swings forward to the ectolophid or mesoconid.

On M_3 (figs. 31, 32), as on the more anterior molars, the metaconid is prominent, descending steeply into the central valley, and the posterior protoconid arm extends toward the posterior flank of the metaconid. The anterior cingular cusp is less distinct than on M_{1-2} but the cingulum itself is long. Although the ectolophid is weak, a mesoconid is present on it. The entoconid is small, and its crest usually curves anterobuccally to the mesoconid, although in one specimen the crest curves posterobuccally toward the posterior cingulum. A hypoconid, more or less distinct depending on wear, occurs on the well developed posterior cingulum.

UPPER CHEEK TEETH: In early wear paracone, metacone, and protocone are well developed and cusped on P^4 (figs. 33, 34). A small protoconule occurs on the protoloph and a large metaconule on the metaloph. The metacone is usually well set in from the posterobuccal margin of the tooth. Paracone and metacone are close together and



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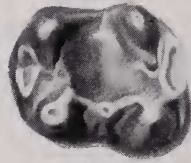
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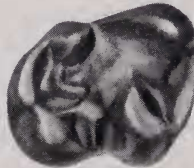
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there is no distinct mesostyle. The hypocone is small and is contacted posterobuccally by the posterior cingulum. The anterior cingulum is short anteroposteriorly but longer transversely than that of *Microparamys*.

The first two upper molars cannot be differentiated from one another with certainty. At first glance M^{1-2} (figs. 35, 36) appear to have the typical sciuravid pattern with protocone and hypocone subequal. However, a closer examination of relatively little-worn teeth shows that in the central basin there is some interconnection of cusps that has not been reported in other Bridgerian sciuravids. The protoloph extends buccally and slightly anteriorly, terminating with a protoconule anterolingual to the protocone, generally similar to the protoloph on M^1 in *S. nitidus*. But in addition a low crest extends posterobuccally from the protocone. This crest is contacted near the center of the central basin by a crest extending anterobuccally from the hypocone. A cuspule frequently occurs at the contact of the two crests. In turn the metacone sends anterolingually a crest, on which the metaconule may be a distinct cusp, to contact the crests from protocone and hypocone near their intersection. Considerable variation occurs in the exact place of contact of the crests with one another, but basically crests from protocone, hypocone, and metacone converge to meet in the central basin. The anterior cingulum is well developed and shelf-like, and the posterior cingulum contacts the hypocone posteriorly. A mesostyle or occasionally two mesostyles occur between paracone and metacone. After wear the cusps and conules in M^{1-2} lose their individuality and the teeth appear more lophate, although the lophs are weak.

The tooth row is not reduced posteriorly, M^3 (fig. 37) being about as wide anteriorly as M^2 . The last molar has a long, well developed anterior cingulum and a prominent paracone, connected by a loph to the protocone. The talon lacks distinctly developed cusps, but a small cuspule on the posterior wall seems to represent a hypocone and the tooth is ridged posterobuccally in the area of the metacone.



Figs. 26-38: Sciuravid sp., occlusal views of teeth. Fig. 26: CM 19618, left P_4 . Fig. 27: CM 19617, left P_4 . Fig. 28: CM 19619, left P_4 or possibly dP_4 . Fig. 29: CM 13219, left lower molar. Fig. 30: CM 13218, left lower molar. Fig. 31: CM 19645, right M_3 . Fig. 32: CM 19614, right M_3 . Fig. 33: CM 19643, left P^1 . Fig. 34: CM 19615, left P^1 . Fig. 35: CM 13210, left upper molar. Fig. 36: CM 13212, left upper molar. Fig. 37: CM 19616, left M^3 . Fig. 38: CM 19644, left dP^1 , probably sciuravid sp. Figs. 29-37, approx. x15; figs. 26-28, approx. x20.

An anteriorly convex loph passes between metacone area and hypocone. A mesostyle is present.

DISCUSSION

The impression that would be gained from a study of the lower molars of this rodent is that it is closely related to *Sciuravus bridgeri*, although the slightly smaller size of the Powder Wash sciuravid might preclude reference to that species. The lower premolar that seems to represent this sciuravid is, however, quite different from the relatively larger, anteriorly wide P_4 of *S. bridgeri*. Complete comparisons cannot be made, since only lower jaws of *S. bridgeri* are known. But whether or not the Powder Wash sciuravid is near *S. bridgeri* in affinities, the structure of the upper molars indicates that it does not represent the genus *Sciuravus*. In the upper teeth of *Sciuravus* the proto-loph and metaloph are basically independent of one another, not becoming joined until the lophs widen following wear.

An Eocene rodent that does show some similarity to this Powder Wash sciuravid in the pattern of upper molar teeth is *Knightomys*, now known from the middle and late Wasatchian. Upper molars of this rodent (Wood, 1965:130-131, fig. 3) resemble those of the Powder Wash sciuravid in having connections from metaloph to both protocone and hypocone. The hypocone and metaloph are less well developed, however, in this early Eocene rodent than in the Powder Wash sciuravid. Lower molars of *Knightomys* are developed on quite a different plan, having much less development of lophs and a different ectolophid-mesoconid structure from that in the Powder Wash sciuravid.

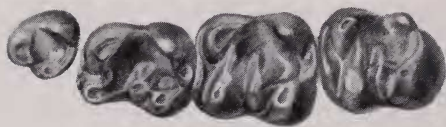
Having only limited information, derived entirely from isolated teeth, on this sciuravid, a precise taxonomic assignment seems out of the question. The species may be related to *Sciuravus bridgeri*, but it is surely not *Sciuravus*. It is an interesting form. By a certain amount of anterior torsion of the lophs its upper molar pattern could be converted into a pattern similar to that found in *Simimys*. It also shows similarities to the smallest Powder Wash rodent described below.

Pauromys Troxell, 1923

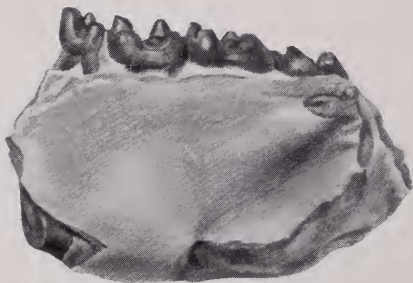
The small Bridgerian rodent *Pauromys* is a relatively poorly known genus from the Bridger Basin, being represented by the lower jaw with P_4-M_3 of *P. perditus* (figs. 39, 40), the type species (Troxell,

TABLE 5
MEASUREMENTS (IN MM.) OF *Sciuravus bridgeri* AND SCIURAVID SP.

Upper teeth	CM 19615	CM 19643	CM 13208	CM 13210	CM 13212	CM 13213	CM 19616	
P ⁴ anteroposterior width	1.24 1.52	1.24 1.55						
M ¹ or M ² anteroposterior width			1.40 1.55	1.43 1.64	1.36 1.55	1.30 1.58		
M ³ anteroposterior width							1.36 1.43	
Lower teeth	USNM 12141	CM 19617	CM 19618	CM 13217	CM 13218	CM 13219	CM 19614	CM 19645
P ₄ anteroposterior width trigonid width talonid	1.55 1.18 1.40	1.30 .87 1.18	1.30 .90 1.18					
M ₁ anteroposterior width trigonid width talonid	1.67 1.18 1.49							
M ₂ anteroposterior width trigonid width talonid	1.77 1.49 1.67							
M ₃ anteroposterior width trigonid width talonid								1.49 1.27 1.27
M ₁ or M ₂ anteroposterior width trigonid width talonid				1.49 1.12 1.33	1.52 1.12 1.27	1.36 1.05 1.33	1.55 1.43 1.24	
Deciduous teeth	CM 19644	CM 19619						
dP ¹ anteroposterior width	1.21 1.12							
dP ₄ anteroposterior width trigonid width talonid			1.18 .68 1.08					



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Figs. 39, 40: *Pauromys perditus*, YPM 13601, type specimen, left jaw with P₄-M₃.
 Fig. 39: occlusal view, approx. x16. Fig. 40: lateral view, approx. x8.

1923), and by a still more fragmentary jaw with M₁₋₃ of *P. schaubi* (Wood, 1959a). The geologic horizon within the Bridger of Dry Creek, from which *P. perditus* came, could be either Bridger B or C. *P. schaubi* is from the Bridger C, in the red layer on Twin Buttes. Although so inadequately known, *Pauromys* has figured in discussions of the Eocene ancestry for later rodents. For example, Stehlin and Schaub (1951:367) considered the genus to be muroid and near the cricetids, and Wood (1959a:5) treated *Pauromys* as a sciuravid that was a possible ancestor for the cricetids. These opinions were based on the lower jaw material mentioned above.

A species of *Pauromys* is the most abundant rodent in the Powder Wash deposits, being represented by at least 800 isolated deciduous and permanent cheek teeth as well as by incisors. Fortunately one maxillary fragment with M¹⁻² and one edentulous jaw of the rodent are also present.

Pauromys sp.

Figures 41-54

SPECIMENS: CM 13143, maxillary fragment, M¹⁻²; CM 19568, jaw fragment; CM 19571, 19640, P¹; CM 13144-13170, 13173, 13175-13182, 13184-13190, 13192,

13194, 13816, M^{1-2} ; CM 13183, 13815, 19639, M^3 ; CM 19574, 19641, 19642, dP^4 ; CM 19569, upper incisors; CM 13142, 19572, 19633, 19634, P_4 ; CM 13038, 13092-13096, 13097-13109, 13111-13115, 13117-13119, 13122-13124, 13126, 13128, 13130-13132, 13134-13141, 13818, 13819, M_{1-2} ; CM 13091, 13116, 13120, 13121, 13125, 13127, 13129, 13133, 13820, M_3 ; CM 19573, 19635, dP_4 ; CM 19570, lower incisors.

DESCRIPTION

The only maxillary fragment (fig. 41) was broken at the alveolar border and has been repaired. However, the piece forming the anterior alveolus of the first cheek tooth, zygomatic root, and infraorbital foramen is intact, accurately showing the relationships of these parts to one another. The infraorbital foramen is well forward in position, rounded ventrally, and slightly elongated dorsolaterad. The foramen does not seem to be enlarged and it probably did not transmit any muscle mass. The zygoma is quite far anterior for a Bridgerian rodent, extending laterad anterior to the alveolus of the first tooth and thus farther forward than in *Sciuravus*. The ventrolateral edge of the zygoma is distinctly ridged. The ridge curves back below the infraorbital foramen and terminates anterior to the first alveolus. It is unlikely that any significant part of the masseter originated anterior to the ridge. Anterior to M^1 there is a small anterolateral alveolus that is confluent with a larger, more posterior opening except medially, where a narrow spicule of bone protrudes between the two openings. Whether one or two premolars occupied these openings is not clear. The small anterolateral opening is more laterally situated than is usually the case for a small P^3 , and has a position more similar to that of the opening for the anterolateral root of P^4 in such a rodent as *Paradjidaumo*. Specimens of P^4 of *Pauromys* sp., although smaller than M^1 , seem to be too long anteroposteriorly to fit the larger posterior opening without overlapping the anterior alveolus. The anterolateral root of P^4 does project anteriorly to some degree. These factors suggest that P^3 was absent in *Pauromys*. The small size of P_4 might be additional evidence for the absence of P^3 . Although the possibility of having a small P^3 in the anterolateral opening cannot be discarded, its presence seems less likely than its absence.

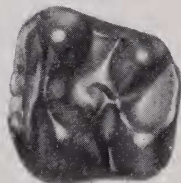
Three roots are present on P^4 , of which the anterolateral protrudes anteriorly, as mentioned above. Specimens of this tooth (fig. 42) are variable in size but are always smaller than M^1 . In outline P^4 is more rounded than M^1 due to the premolar's smaller hypocone. The latter, however, is better developed than on P^4 of *Sciuravus eucristadens* and



41



42



43



44



45



46



47

the unnamed sciuravid. The paracone and metacone are close together. Between them there may be a small mesostyle, although this is absent in some specimens. A small protoconule occurs on the protoloph and a more strongly developed metaconule on the loph from metacone to protocone. At about the midline of the anterior cingulum a short loph extends posteriorly to contact the protoloph at the protoconule. The hypocone varies somewhat in size and connections. When large the hypocone usually has a crest meeting the loph from the metacone, but when smaller it seems to lack the crest. The metacone is the most prominent cusp of P^4 and is the last cusp to be worn down.

The first two upper molars (figs. 43, 44) are basically quadrate teeth having well developed paracone, metacone, protocone, and hypocone. Protoloph and metaloph, seldom with more than a suggestion of conules, are present. Usually one but sometimes two mesostyles occur. If two, one may be either posterior or medial to the other. There is an anterior and a posterior cingulum. In addition to this basic pattern there are crests in the central basin that show some similarity to the added crests in the unnamed sciuravid. The crests, though variable, usually include one directed anterobuccally from the metaloph and one directed posterobuccally from the posterior flank of the protocone. The latter crest is the more variable of the two, and is often weak or absent. The two crests contact one another at their lateral tips or are connected by a short longitudinal crest. Frequently a small cuspsule is present at the junction of the crests.

The last molar (fig. 45) is smaller than M^{1-2} , more triangular than quadrate because it has a smaller hypocone, and, as is often true of M^3 , variable in size. The anterior cingulum is long transversely. Paracone and protocone are well developed and connected by a protoloph. The mesostyle can usually be distinguished. The hypocone is smaller than the protocone but is usually a distinct cusp. The metacone is sometimes distinct but often it merges with the posterior cingulum. Variable cuspsules occur as swellings on this cingulum. Sometimes a loph or row of cuspsules occurs between the metacone and the protocone, or a loph may occur between the metacone and the hypocone.

←
Figs. 41-47. *Pauromys* sp. Fig. 41: CM 13143, oclusal view of right maxilla with M^{1-2} , approx. x15. Figs. 42-47: oclusal views of upper teeth, approx. x20. Fig. 42: CM 19640, left P^1 . Fig. 43: CM 13181, left upper molar. Fig. 44: CM 13162, left upper molar. Fig. 45: CM 13815, right M^3 . Fig. 46: CM 19642, right dP^1 . Fig. 47: CM 19641, left dP^4 .

The teeth that seem to be dP^4 (figs. 46, 47) of *Pauromys* are more molariform than P^4 in having: (1) a better developed hypocone subequal to the protocone; (2) more widely separated paracone and metacone; and (3) a complete metaloph. Distinct conules seem to be lacking from protoloph and metaloph. Not even in the relatively unworn specimens of dP^4 does there seem to be a crest between protocone and metaloph, although several relatively little worn specimens of dP^4 show a short process extending anterobuccally from the metaloph into the central valley. As often in dP^4 of rodents, the anterior cingulum protrudes more than in P^4 and the mesostyle is elongated anteroposteriorly rather than being a rounded cuspule.

An incomplete jaw having a broken incisor but lacking cheek teeth, CM 19568, is referable to this small species. The tiny jaw has a distinct ventral keel below the symphysis. The single mental foramen is in a line anterior to P_4 as it must have been in *Pauromys perditus*. In *P. schaubi* this foramen is larger and occurs below the trigonid of P_4 . The anterior border of the masseteric fossa is in a line approximately below the talonid of M_1 . The lateral surface of the jaw is poorly preserved in *P. perditus*, YPM 13601, but the fossa seems to have about the same position in that species, whereas in *P. schaubi* the fossa reaches forward a little farther, having its anterior border below the middle of M_1 .

The five specimens P_4 are variable in size, but P_4 (figs. 48, 49) is always small relative to M_{1-2} . Protoconid and metaconid are both present on the trigonid, the latter being dominant. The trigonid basin is closed posteriorly by a loph between the cusps. The central valley is very small. The ectolophid is weak but a mesoconid is present on it, sometimes cusplate and sometimes elongated transversely. The distinctly cusplate entoconid is not crested but is contacted by the posterior cingulum. Although Troxell (1923) described P_4 of *P. perditus*, YPM 13601, as having but one cusp on the trigonid, reexamination of the specimen shows that both protoconid and metaconid are present, although small. Even the smallest P_4 of *Pauromys* sp. from Powder Wash is larger than P_4 of *P. perditus*. Also P_4 of *Pauromys* sp. has a relatively larger trigonid featuring a larger and better developed metaconid.

The first lower molar can be differentiated from M_2 on the basis of the more elongate, anteriorly narrower shape of M_1 as opposed to a more quadrate appearance of M_2 . The pattern of M_{1-2} (figs. 50-52) resembles that of the corresponding teeth of *P. perditus*. The anterior

cingulum is well developed, usually longer transversely on M_2 than on M_1 , and tends to be cusperate at its buccal end. The posterior protoconid arm is long, usually closing the trigonid basin on M_2 , but frequently shorter and leaving the basin open posteriorly on M_1 . The ectolophid is weak or absent, but the mesoconid is well developed. On M_1 the mesoconid varies from mostly rounded, with only a slight elongation, to elongated with a crest as well developed as that on M_2 . The entoconid is crested, although not strongly. Usually the crest extends posterobuccally to contact the posterior cingulum near the cingular swelling that represents the hypoconulid. Less frequently the crest crosses the tooth transversely to or toward the hypoconid.

The last molar (fig. 53) is smaller than M_2 , but its pattern has most of the same elements as that tooth: transversely long anterior cingulum, long posterior arm of protoconid closing the trigonid basin, elongated mesoconid, and weak or absent ectolophid. The main distinction of M_3 is its usual lack of an entoconid crest or hypolophid, the distinct entoconid usually being connected directly to the posterior cingulum. In one specimen the entoconid is crested as well as having a connection with the posterior cingulum. Another variation seen in one specimen of M_3 is presence of a cuspule in the valley between entoconid and hypoconid.

The lower deciduous premolar (fig. 54), known from eleven specimens, is relatively more elongate than P_4 . Short lophs from the protoconid and metaconid unite posterior to a small trigonid basin, which has a cuspule in its anterior exit. This cuspule is gone on well-worn dP_4 . The ectolophid is either poorly developed or, more usually, absent, although the distinct mesoconid is present and often elongated transversely. The entoconid is crested with the crest extending toward the hypoconid most frequently, paralleling the posterior cingulum. Sometimes the crest extends more posteriorly and contacts the posterior cingulum. This tooth is more molariform than P_4 in elongation of the mesoconid and the amount of cresting of the entoconid. Its generally elongated form and the shape of its trigonid are fairly common characters for a rodent dP_4 .

The incisors of *Pauromys* are narrow transversely and have convex anterior surfaces. The sides of the upper incisor are essentially flat and taper toward one another posteriorly. The lower incisor has a flat medial surface and a slightly convex lateral one.



48



49



50



51



52



53



54

DISCUSSION

Taxonomic treatment of this small rodent has presented difficulties due in part to the incomplete record of *Pauromys*, the rodent genus to which it seems to be referable. *Pauromys* sp. resembles *P. perditus* in most features that can be compared, including lower molar pattern and lower jaw structure. It differs mostly from the one known specimen of *P. perditus* in having a relatively larger P_4 with better developed trigonid. The size of P_4 in *Pauromys* sp. may be closer to that of *P. schaubi*, as inferred from the size of the alveolus of P_4 in the one known jaw of the latter. *Pauromys schaubi* is somewhat larger than *P. perditus* and has a different position of the mental foramen on the jaw. The known, admittedly inadequate, morphological evidence on *Pauromys* does not seem to allow definite reference of the Powder Wash specimens to either previously named species. The geologic evidence is inadequate also, although *Pauromys* sp. might be older than the Bridger Basin species. Perhaps a better representation of the Bridger Basin species would show that populations of which they were part grade morphologically into the Powder Wash sample. Of two lines of action, referring the Powder Wash specimens to a new taxon or leaving them unnamed, the latter course is here hesitantly taken, due mostly to the weight placed on the range of variation within the Powder Wash sample.

Upper teeth of *P. perditus* and *P. schaubi* are unknown, and it is possible that the upper teeth of these species differ from those of *Pauromys* sp. This possibility is regarded here as improbable because the close similarity between *P. perditus* and *Pauromys* sp. in lower molar structure would make different upper molar patterns unusual and unexpected functionally.

Previous workers have considered the structure of the lower molars and reduction of P_4 of *Pauromys* to suggest that this small North American rodent was ancestral to various later forms, especially to cricetids. These possibly ancestral characters occur in *Pauromys* sp., which shows in addition some advance in the zygomasseteric structure, although the origin of the masseter muscle was probably still limited to the ventral or ventrolateral surface of the zygoma. This is certainly

←
Figs. 48-54. *Pauromys* sp., occlusal views of lower cheek teeth. Fig. 48: CM 19634, right P_4 . Fig. 49: CM 19633, right P_4 . Fig. 50: CM 13095, right molar, probably M_1 . Fig. 51: CM 13106, left molar, probably M_2 . Fig. 52: CM 13102, right lower molar. Fig. 53: CM 13120, right M_3 . Fig. 54: CM 19635, right dP_4 . Figs. 48, 49, 54, approx. x30; figs. 50-53, approx. x20.

TABLE 6
MEASUREMENTS (IN MM.) OF *Pauromys*

Upper teeth	CM 13143	CM 19640	CM 13149	CM 13162	CM 13164	CM 13181	CM 13183	CM 13815	
P ⁴ anteroposterior		.81							
width		.84							
M ¹ anteroposterior		.99							
width		1.05							
M ² anteroposterior		.99							
width		1.05							
M ³ anteroposterior							.93	.99	
width							.96	.93	
M ¹ or M ² anteroposterior			.93	.93	.99	1.12			
width			.99	.96	.99	1.12			
Lower teeth	YPM 13601	AMNH 11722	CM 19633	CM 19634	CM 13093	CM 13100	CM 13111	CM 13091	CM 13120
P ₄ anteroposterior	.56		.74	.62					
width trigonid	—		.53	.56					
width talonid	.56		.68	.65					
M ₁ anteroposterior	.99	1.08							
width trigonid	.71	.84							
width talonid	.81	.90							
M ₂ anteroposterior	.99	1.15							
width trigonid	.90	.99							
width talonid	.96	1.05							
M ₃ anteroposterior	1.05							1.08	.99
width trigonid	.87							1.02	.90
width talonid	.78							.96	.87
M ₁ or M ₂ anteroposterior					1.05	1.05	1.05		
width trigonid					.87	.81	.93		
width talonid					.96	.90	1.02		

TABLE 6, Cont'd.

Deciduous teeth	CM 19642	CM 19635
dP ⁴ anteroposterior	.81	
width	.81	
dP ₄ anteroposterior		.84
width trigonid		.50
width talonid		.71

the most progressive zygomaseteric region of the maxilla that has been found in a North American Bridgerian rodent. It is interesting that this forward position of the zygoma is accompanied by only a small amount of anterior migration of masseter attachment of the lower jaw. Reduction of the upper premolars also characterizes *Pauromys* sp., in which P⁴ is small, though its cusps are well developed and distinct, and P³ is either absent or very much reduced.

While showing these advanced characters *Pauromys* is still basically a sciuravid, having the typically quadrate upper molars and crested lower molars of the family. Reduction of the premolars has advanced farther than in most other sciuravids, although the poorly known *Sciuravus rarus* (Wilson, 1938: 136-137) and another Bridgerian sciuravid (Dawson, 1962) show that some other sciuravids were undergoing various types of premolar reduction. The early Eocene *Knightomys* has a pattern in upper and lower molar teeth (Wood, 1965:127-132) that could develop, following strengthening of the crests, into something similar to that in *Pauromys*. Probably the stock leading to this rodent genus was close to *Knightomys*.

Pauromys sp. and the unnamed sciuravid of Powder Wash are similar in having upper molar patterns previously unknown in North American Bridgerian rodents. The special crests in the central basin of M¹⁻² in these rodents are probably not new structures but rather are strengthened retentions from an earlier Eocene ancestor near *Knightomys*. These crests may include remnants of cresting between metacone and protocone found also in the ischyromyids *Microparamys* and *Franimys*. The crests in *Pauromys* sp. and the sciuravid not only reflect a retention of older structures but also have the potential for developing into the connection, or mure, between protoloph and metaloph that is found in such later rodents as *Simimys*, cricetodontines, and zapodids. The gap in time and morphology between these

Powder Wash sciuravids and possibly allied myomorphs is, however, too great to allow more than a suggestion of these affinities to be made at this time.

GEOLOGIC AGE OF POWDER WASH LOCAL FAUNA

In a recent essay Wilson (1967) clearly states the dangers of basing an age determination for a fossil assemblage on evidence from one taxon alone, even a taxon as broad as the order Rodentia. The dangers are here recognized, but it is desirable to record the suggestions that rodents make as to the age of the Powder Wash fauna so that this evidence can contribute its part after other elements of the fauna have been studied.

Generally the entire mammalian fauna has a Bridgerian appearance. More specifically, Burke (1935) considered his upper fossiliferous zone—that is, the zone of the Powder Wash local fauna—to contain a “lower Bridger faunal assemblage.” The only previous detailed study of a taxonomic group from Powder Wash was that of Gazin (1958), who included the Powder Wash species in his work on middle and upper Eocene primates. Although evidence from these primates was somewhat inconclusive (two species limited to Bridger B; one species, poorly known at Powder Wash, otherwise only from Bridger D; one referred to a Bridger D species although the Powder Wash individual is smaller; two species restricted to the Powder Wash local fauna), Gazin considered the level of the fauna to be a “lower (?) Bridger equivalent.” What do the rodents add to the estimate of age for the fauna?

On the family level, ischromyids and sciuravids, the two families represented, range through the entire Eocene. Thus, their presence does not contribute in detail. Perhaps more significant on this level is an absence—there are no cylindrodontids among the Powder Wash rodents. No early Eocene cylindrodontids are known, but the cylindrodontid *Mysops* is characteristic of the middle Eocene, and by the late Eocene the family exhibited some diversification.

On the generic level, all genera of Powder Wash rodents except *Pauromys* occurred also in the early Eocene. All of them are previously known throughout the Bridgerian with the possible exception of *Pauromys*, which may or may not have an early Bridgerian record.

On the specific level other evidence appears. *Pseudotomus* and *Paramys* from Powder Wash cannot be referred definitely to Bridger-

ian species because of the smaller size of the Powder Wash individuals. In this smaller size and in the narrower incisor found in *Paramys* from Powder Wash, resemblance to early Eocene species is seen. *Sciuravus eucristadens* is known only from Powder Wash. Some of its differences from *S. nitidus*, the typical Bridgerian sciuravid, such as the appressed paracone and metacone of P⁴ and crowded cusps of the lower molars, are characters of the late Wasatchian *Sciuravus wilsoni*. The specimens of *Pauromys* from Powder Wash appear to be slightly more primitive than *P. perditus* in having a less reduced P₄. The *Microparamys* of Powder Wash, on the other hand, seems to be referable to *M. minutus*, a species ranging through the Bridgerian.

The following tabulation gives the critical points that might apply to an age determination for the Powder Wash local fauna.

RODENTS FROM POWDER WASH

Pseudotomus near *P. robustus*
Paramys near *P. delicatus*

Microparamys minutus
Sciuravus eucristadens

sciuravid sp.

Pauromys sp.

SUGGESTIONS AS TO AGE

Near species ranging through Bridgerian but Powder Wash specimens smaller and like early Eocene species in some ways.

From entire Bridgerian.
 Powder Wash only; morphology shows some similarity to late Wasatchian species.

Evolutionary level near that of *Sciuravus bridgeri*, an early Bridgerian species.

Other species from either Bridger B or C and from Bridger C. No definite suggestions other than Bridgerian.

RODENTS ABSENT FROM POWDER WASH

Cylindrodontids

Occur in entire Bridgerian.

In total, the evidence points toward an early Bridgerian age, thus corroborating the estimates of Burke and Gazin. To be more specific is hazardous, but if age were the only factor responsible for taxonomic differences, there might be found faint suggestions from *Pseudotomus*, *Paramys*, *Sciuravus eucristadens*, and perhaps from the absence of cylindrodontids, that the Powder Wash rodents are older than those typically found in the Bridger B of the Bridger Basin.

But of course age is not the only factor accounting for faunal differences, and ecological factors could account for the relatively minor taxonomic differences between the Powder Wash taxa and those from the Bridger Basin. The stream border and lake margin facies that are probably represented in the deposits at Powder Wash

may have a different but contemporaneous fauna from that of the more typically flood-plain deposits of the Bridger Basin. Absence of cylirodontids could represent facies differences also. Perhaps *Microparamys minutus* was more tolerant ecologically than the other taxa at Powder Wash and ranged through stream border and also flood-plain habitats.

COMPOSITION OF POWDER WASH RODENT ASSEMBLAGE

The six rodent species vary greatly in numbers in the Powder Wash deposits. By far the most abundant is the smallest species, *Pauromys* sp., which is known from only one maxilla and one jaw but also from at least 800 isolated cheek teeth. The number of individuals represented is probably near 50 ($\frac{1}{2}$ x number of right M^{1-2}). Next in order of abundance is *Sciuravus eucristadens*, with ten maxillae, 13 jaws, and about 235 isolated cheek teeth. Following this, *Microparamys* is known from about 120 cheek teeth, sciuravid sp. from about 80 cheek teeth, *Paramys* from one maxilla, one jaw, and 18 cheek teeth, and *Pseudotomus* from five teeth.

It is difficult to estimate for a deposit such as that at Powder Wash how much the abundance of fossils represents true abundance in the area, because there may have been strongly selective action taking place before burial. The small size of most mammals in the Powder Wash deposit, for example, indicates that rodents the size of *Pseudotomus* might have been selected against by the factors affecting deposition. On the other hand, it is obvious that *Pauromys* must have been abundant in the area, and *Sciuravus eucristadens* moderately so.

All taxa except *Pseudotomus* are represented by deciduous as well as permanent teeth. For *Pauromys* sp., for example, approximately 30 of the 800 isolated teeth are deciduous, as are approximately 25 of the 235 isolated teeth of *S. eucristadens*. Relative to the total number of specimens the proportion of deciduous teeth is highest for *Paramys*, of which there are six deciduous teeth in the total of 18 isolated teeth. It is tempting to use this proportion as evidence that the habitat may have been more favorable for young than for mature individuals of that genus. However, the total number of specimens of *Paramys* is so small that this proportion of deciduous teeth should probably not be regarded as significant, for chance preservation of a few immature individuals could account for the higher proportion.

DIVERSITY AMONG EOCENE RODENTS

Within the Eocene there are now three localities that have been well sampled for microfauna, by the use of washing and screening techniques. These are the earliest Eocene Four Mile fauna of Colorado (McKenna, 1960), the Powder Wash fauna of Utah, and the Uintan Badwater fauna of Wyoming (Black and Dawson, 1966). Since similar collecting techniques were used, the faunas might be comparable for composition.

FOUR MILE (several quarries) Early Wasatchian	<i>Paramys</i> sp. A (several taxa?); <i>Paramys</i> sp. B; <i>Paramys</i> sp.; rodent gen. and sp. indet.
POWDER WASH (one quarry) Early Bridgerian	<i>Pseudotomus</i> ; <i>Paramys</i> ; <i>Microparamys</i> ; <i>Sciuravus</i> ; sciuravid sp.; <i>Pauromys</i> sp.
BADWATER (several quarries) Uintan	<i>Ischyrotomus</i> ; <i>Leptotomus</i> ; <i>Rapamys</i> ; <i>Microparamys</i> ; ? <i>Plesi-</i> <i>spermophilus</i> ; ? <i>Pseudocylindrodon</i> ; <i>Sciuravus</i> ; sciuravid sp.; eomyid sp.; rodent <i>incertae sedis</i> .

There are surely ecological restrictions on all these samples. However, these three similarly collected samples can be used to illustrate the general flowering of rodents during the Eocene. Especially notable are: (1) increase in number of taxa, with the increase from early Bridgerian to Uintan being most prominent; (2) increase in diversity, illustrated by presence in the early Wasatchian of ischyromyids only, by ischyromyids and sciuravids in the Bridgerian, and by ischyromyids, sciuravids, cylindrodontids, and eomyids in the Uintan.

CONCLUSIONS

Six species of rodents occur in the early Bridgerian Powder Wash local fauna of northeastern Utah. Three are Ischyromyidae, *Pseudotomus* near *P. robustus*, *Paramys* near *P. delicatus*, and *Microparamys minutus*; and three are Sciuravidae, *Sciuravus eucristadens*, an unnamed sciuravid, and *Pauromys* sp.

Of the ischyromyids, *Pseudotomus* and *Paramys* do not contribute new information pertinent to phylogeny. The specimens of *Microparamys minutus*, however, add to the previously known morphology of this rodent and show some similarities in M^3 to more primitive early Eocene ischyromyids such as *Franimys*.

The sciuravids are phylogenetically more interesting. *Sciuravus eucristadens* may be allied to the Uintan *S. powayensis* of California. The unnamed sciuravid and *Pauromys* sp. have a crested pattern of the upper molars that was previously unknown in Bridgerian sciuravids. Somewhat similar crests are known in the early Eocene sciuravid *Knightomys*. Such cresting has the potential of developing into the connecting crests between protoloph and metaloph of some later rodents, especially of some among the myomorphs. The gap in time and morphology between these early Bridgerian rodents and the more advanced forms is still too great, however, to allow the tracing of relationships. *Pauromys* sp. is significant also in having an advanced, anteriorly situated zygoma and a reduced P_4 .

Some of the Powder Wash rodents show morphological differences from related forms typical of the early Bridgerian of the Bridger Basin, and the Powder Wash faunal composition differs also from that typical of the Bridger Basin. These differences could be caused by slight age differences or by ecological factors. If geologic age is the major contributing factor, the Powder Wash local fauna is probably older than the well-known early Bridgerian faunas of the Bridger Basin. If ecology, the differences in the rodent faunas may reflect the stream-side and lake-margin habitat of Powder Wash as opposed to the predominantly flood-plain habitat of the Bridger Basin.

The Powder Wash local fauna represents a stage in rodent development between early Wasatchian faunas, in which all rodents are ischyromyids, and Uintan faunas, in which ischyromyids, sciuravids, cylindrodontids, and eomyids illustrate a marked taxonomic diversity among rodents.

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